FACTORS AFFECTING ACTIVITY AND BURROWING HABITS OF THE PINK SHRIMP, PENAEUS DUORARUM BURKENROAD

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The purpose of this study was to determine the effects of light, temperature, salinity, fatigue, persistent daily rhythms, availability of food, bottom types, and bottom water currents on the daily activity and burrowing habits of adult pink shrimp (*Penaeus duorarum*), and to attempt an estimate of their relative importance. Results of modified *in situ* and controlled observations were combined to present a better assessment of behavior in the natural habitat.

Some of the factors influencing the activity and burrowing habits of certain penaeid shrimp have been investigated directly or indirectly in several previous studies. Williams (1958) examined the relation between substrate and burrowing; Eldred (1958) noted the effects of colored light and molting; Williams (1955) and Eldred *et al.* (1961) suggested the effects of low temperature; Wheeler (1937) and Racek (1959) attempted to elucidate the influence of lunar periodicity on activity; Egusa and Yamamoto (1961) demonstrated the effects of low oxygen tension; Dall (1958), Ghidalia and Bourgois (1961), Aaron and Wisby (1964), and Fuss (1964) referred to the possible influence of moon phase or light level. The lack of agreement among some of the above works, particularly concerning the effects of light and lunar periodicity, prompted this investigation.

It is now well established that pink shrimp do burrow into the substrate and are usually active at night (Eldred *et al.,* 1961; Fuss, 1964). Methods of burrowing have been described by Dall (1958) for *Metapenaeus mastersii;* by Egusa and Yamamoto (1961) for *Penaeus japonicus;* and by Fuss (1964) for *P. duorarum.* All of the reported burrowing methods are generally similar.

The observations and experiments reported here are part of a general study by the U. S. Fish and Wildlife Service, Bureau of Commercial Fisheries Gear Research Station in Panama City, Fla., to learn the basic behavior of adult penaeid shrimp.

MATERIALS AND METHODS

In the initial phases of this study the modified *in situ* approach was chosen to eliminate the effects of habitat modification. We first made gross observations on the methods of burrowing, the degree of bottom penetration, and general diurnal cycles of activity (Fuss, 1964), none of which required controlled experiments. As the study progressed we decided to incorporate a series of controlled and partially controlled aquarium observations to supplement field data and provide a quantitative measure of the effects of certain factors on the behavior of *P. duorarum.*

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The limitations of data obtained from aquarium studies in the interpretation of gross behavior have been emphasized by a number of workers (Walford, 1958; Kavanau, 1964; and others), and are presented here to assist in the evaluation of non-controlled observations. The data, although literally quantitative, are primarily used here in a qualitative sense through two-fold or multiple grouping as described by Simpson, Roe and Lewontin (1960).

Shrimp were obtained by night trawling in St. Andrew Bay, Fla., and held in a large submersible cage at the Station's Behavior Studies Facility. Recently-captured animals were used in all observations and experiments, and their total lengths recorded. All shrimp not in burrows were considered active. We arbitrarily included in this grouping all individuals that were swimming, moving about, or motionless on the substrate.

Controlled experiments were carried out with 35.6 by 20.3 by 25.4 cm. aquaria fitted with tailored plastic covers to regulate the entry of light. During the colder months, water temperature in the aquaria was partially controlled with submersible heaters. Each aquarium had about 6 cm. of washed beach sand and was filled with constantly aerated bay water ranging from 23‰ to 33‰ salinity. Observations were made hourly during 24-hour periods, using a red filtered flashlight at night.

A 38.1 by 30.5 by 30.5 cm. aquarium, contained in a light-proof black box with a light-lock viewing hood, was used for the 72-hour fatigue experiments where control of light was essential. Observations were made every two hours, and observation illumination was provided with two small red lights built into the aquarium cover.

We made non-controlled observations at the Behavior Facility in 3 to 4 meters of water, using a static underwater observation chamber (SUOC), which was previously described by Fuss and Ogren (1965). Shrimp were placed in 1-meter-square bottomless metal frame cages covered with small-mesh netting. The cages were attached to underwater viewing ports by funnel-shaped extensions of webbing on one side and were held in position by driving the cage legs into the substrate. Night illumination was by underwater flood lights fitted with red filters and controlled by switches inside the chamber. Six measured shrimp were placed in each cage and observed at hourly intervals during 24-hour periods. SUOC observations were considered as modified *in situ* observations.

Water current orientation observations were made at the entrance to St. Andrew Bay and in the vicinity of Egmont Key, Fla., using self-contained underwater breathing apparatus. A "Burrow Angle Protractor" was used to measure the angle resulting from the intersection of the water current axis and the anterior-posterior line of the burrowed shrimp. Individual measured shrimp were released about 1 m. above the bottom and each kept under surveillance by a diver until it began burrowing. The point of origin of the protractor was placed directly over the tip of the tail of the burrowed animal. The protractor was then orientated by using the current tell-tale (a piece of nylon string with a plastic stabilizer at the tip to dampen yaw) so the Y-axis of the instrument and the axis of the current coincided. The angle of burrowing was then measured to the nearest 5° by lining up the indicator arms with the anterior-posterior axis of the burrowed shrimp. Burrowing angles were recorded as degrees left or right of the water current axis when facing the current. A current velocity reading was taken as close as possible to the

substrate-water interface with an Ekman-Merz type meter before and after the release of each five shrimp.

Salinity was determined by a density hydrometer or recorded continuously with an Industrial Instruments/Minneapolis-Honeywell single point strip chart salinity recorder-indicator [2] having a CELVH10270 conductivity cell. Incident light was recorded *in situ* or on the surface with a SeaTec model 210 Low Level Light
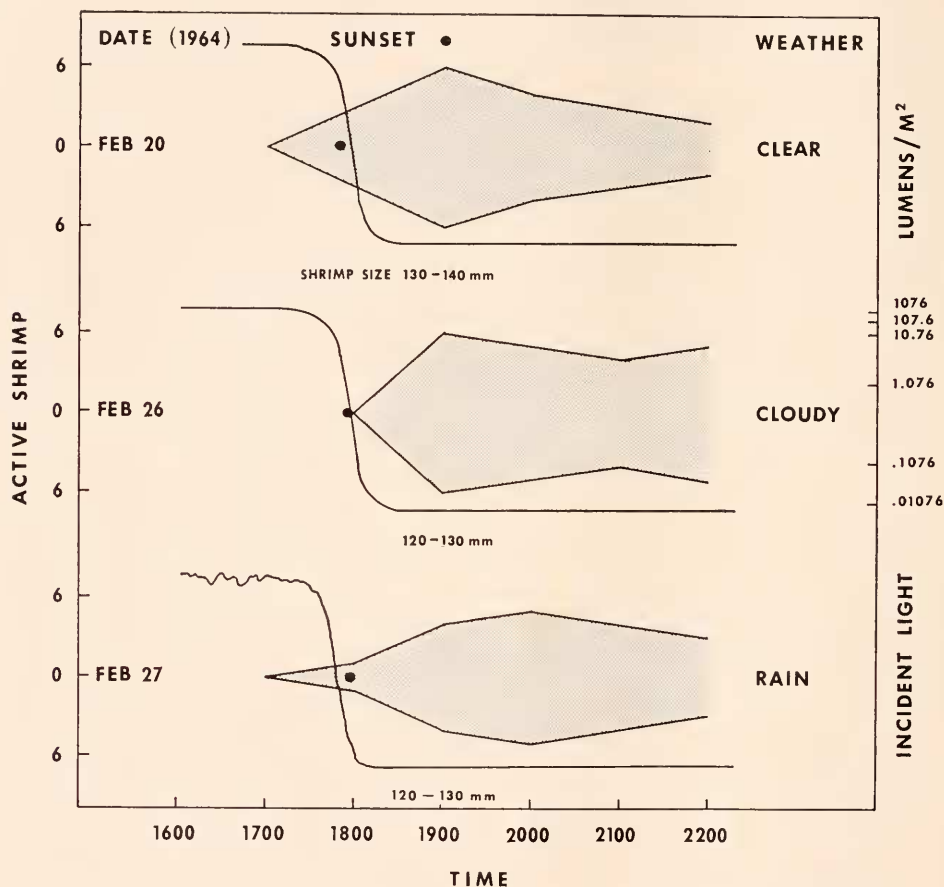

FIGURE 1. The emergence of burrowed shrimp in relation to decreasing *in situ* incident light. Left ordinate and shaded area = activity; right ordinate and trace recording = incident light.

Recorder with a range of 0.01076 lumens per m.[2] to 10764 lumens per m.[2]. Subsurface temperature measurements were taken with an Applied Research Associated Electronic Thermometer and precision grade thermometers attached externally to SUOC observation ports.

For certain observations on various bottom types and during current-orientation

[2] Trade names referred to in this publication do not imply endorsement of commercial products.

studies, shrimp activity was recorded with either a Bell and Howell or a Bolex 16 mm. underwater motion picture camera.

Results

Activity Cycles

Light. SUOC and aquarium observations indicate that light is the most important single factor in the regulation of activity of adult (for this study, 80–180 mm., total length) pink shrimp. A total of 224 shrimp were observed over 24-hour periods at hourly intervals, with only 12 individuals showing any activity
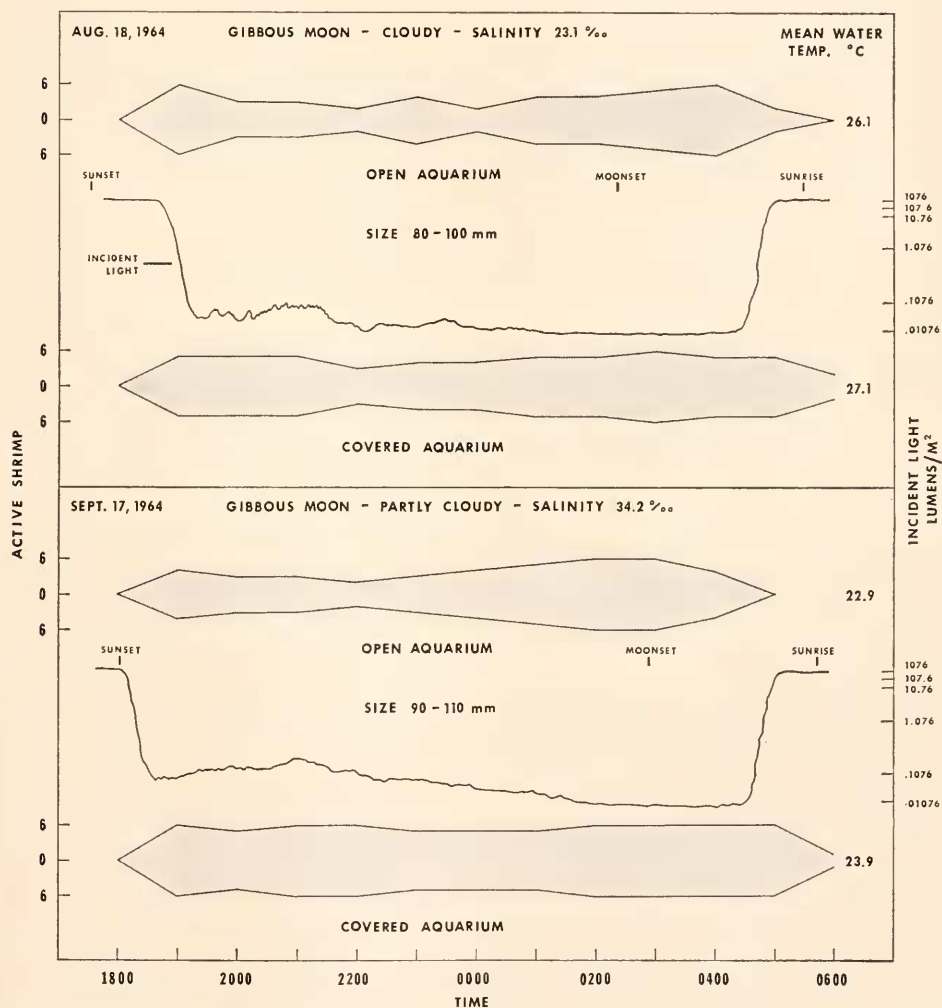

FIGURE 2. The effects of moonlight on the activity of pink shrimp.

during daylight hours. Of these 12, six were in one aquarium experiment when water temperature was allowed to exceed 33° C.

In the initial phases of the study, light-metering equipment was not available, but the effect of daylight was obvious. Shrimp held in cages on the bay bottom remained burrowed during the day and began to emerge around sunset, regardless of weather conditions. With the acquisition of a low-level light meter it was possible to demonstrate this burrowing activity in response to light shown in Figure 1. The sensitivity of the light meter, however, was not sufficient to detect fluctuations in light after sunset at the observation depth. By the time the shrimp were most active, about one hour after sunset, the meter showed a minimum reading and further correlation of light and activity was impossible. The early evening readings indicated that activity was fairly well established when light levels had decreased to 1.076–0.01076 lumens per m.[2]

To test the effects of moonlight, shrimp were held in aquaria in a secluded area of St. Andrew State Park and observed hourly with a red-filtered flashlight during
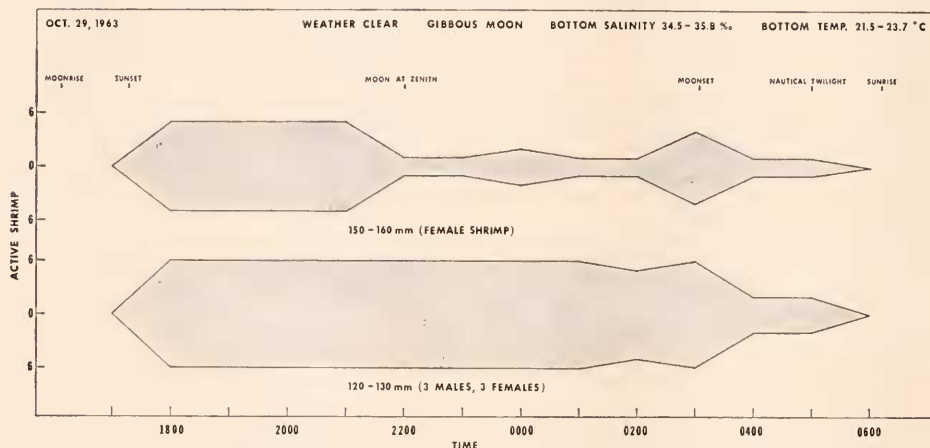

FIGURE 3. The apparent effect of moonlight on two size groups of pink shrimp at a 3-m. depth.

two periods between first quarter and full moon. The location of the observations eliminated the possible influence of extraneous light and allowed for maximum use of the light recorder. The results are shown in Figure 2 and illustrate the restrictive influence of moonlight on night activity. Maximum activity did not take place until after moonset when the meter again showed a minimum reading. These recordings, however, do show the effect of moonlight at intensities of 0.1076–0.01076 lumens per m.[2] and help to document the relative importance of moonlight as a controlling factor in night activity. The covered aquaria in each observation series were intended as controls, but the slight decrease of activity noticeable during the early evening suggests the presence of light leaks due to improperly fitted covers.

Figure 3 shows what appears to be a moonlight effect on relatively large female shrimp (150–160 mm.) held in a cage on the bay bottom. Although the sample is too small to generalize, size seems to be a factor in response to light, with larger individuals being the more sensitive.

Temperature.   SUOC and aquaria observations showed a positive correlation between water temperature below 26° C., and night activity of pink shrimp.   The effect of temperature below about 14°–16° C. seems to mask or modify the expected night behavior patterns related to light intensity noted above.   Below 14° C., shrimp show a strong tendency to remain burrowed regardless of light levels or moon phase.   Table I and Figure 4 show that an activity ratio of 50% or less can be expected below 14°–16° C.   Figure 5 points out the degree of control exerted by low temperatures and the reversible effect of temperature fluctuations at or near 10° C.   It was possible to control activity by regulating aquarium heat.

TABLE I

Random aquarium observations from November, 1963, to June, 1964, showing ratios of active to burrowed shrimp for various temperatures.
Size range: 80–175 mm. (total length)

Water temperature C.°	Active shrimp (nonburrowed)	Total shrimp observed	Activity ratio
30	5	6	0.83
29	16	18	0.89
28	21	24	0.88
27	27	30	0.90
26	27	30	0.90
25	30	36	0.83
24	39	48	0.81
23	124	162	0.77
22	112	150	0.75
21	40	54	0.74
20	47	60	0.78
19	38	50	0.76
18	55	70	0.79
17	68	94	0.72
16	112	180	0.62
15	82	168	0.49
14	24	48	0.50
13	42	88	0.48
12	25	60	0.42
11	15	60	0.25
10	10	114	0.09
9	0	42	0.00
8	0	42	0.00
7	0	30	0.00

On one occasion during a dark aquarium experiment water temperature was allowed to rise to 33.5° C.   The shrimp were not actively swimming but remained motionless on the bottom and did not burrow when the hood was raised and light admitted.   With decreasing temperature these animals began to burrow, but all (six shrimp, 80–90 mm.) were not covered until the water reached about 28.5° C.

An apparent size effect was also noted in the response of shrimp to low temperatures.   SUOC data presented in Figure 6 show a tendency for relatively larger shrimp (larger than 140 mm.) to be less active at low temperature than smaller individuals.   Figure 6 also demonstrates the rather typical and pronounced winter
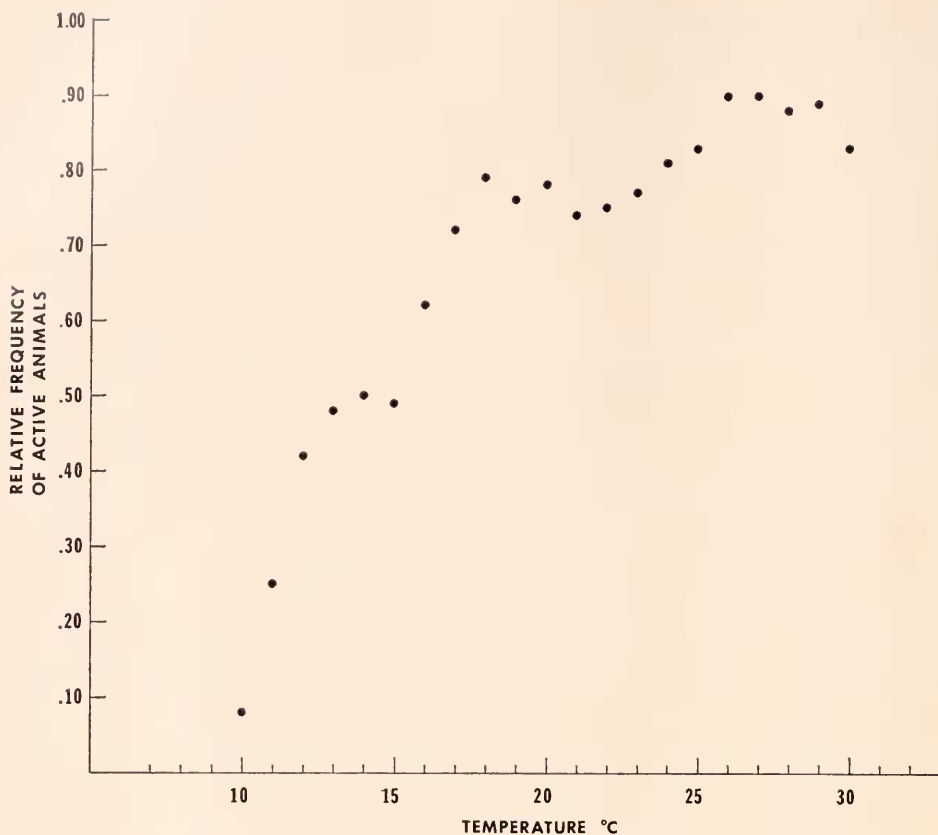
FIGURE 4. Relative activity of pink shrimp at various observed temperatures under controlled conditions (data taken from Table I).
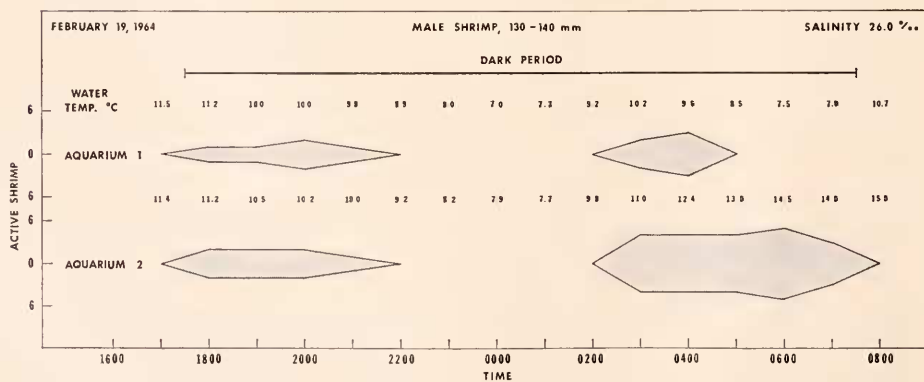

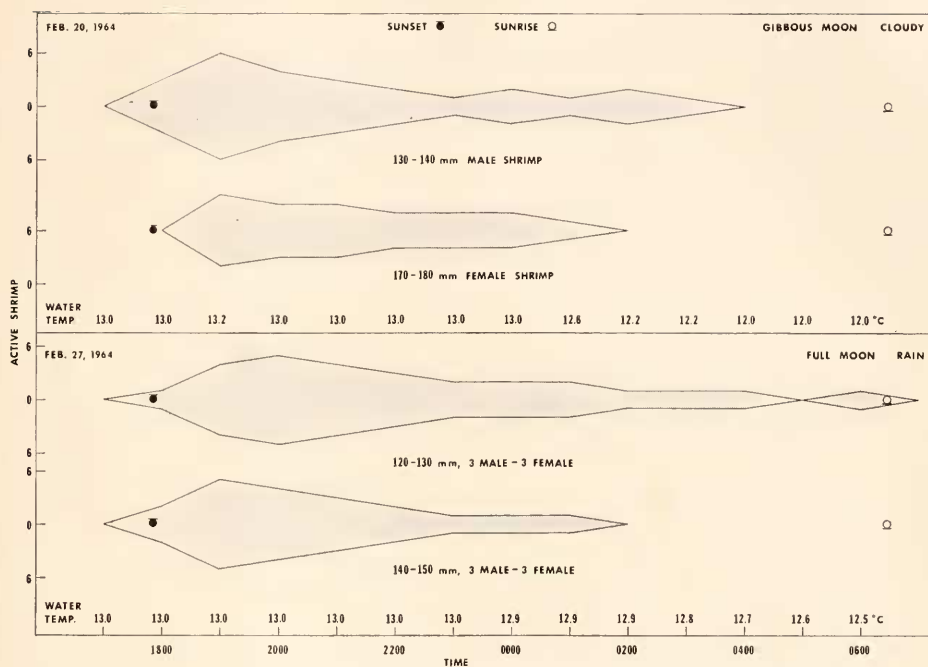FIGURE 5. The effects of low temperature on shrimp activity.

FIGURE 6.   The apparent effect of low temperature on four size groups of
pink shrimp at a 3-m. depth.

activity pattern of a burst of activity immediately after sunset followed by a gradual
decline.

Salinity.   Clear correlations were not noted between modified *in situ* activity
and daily salinity fluctuations in the ranges observed (18.7–35.8‰).   The largest
recorded salinity excursion during any 24-hour period was 7.5‰.   Salinity changes
in the observation area were frequently rapid because of movements of a salt-water
wedge associated with tides but did not produce corresponding changes in activity.
There is a suggestion of a slight tendency for increased activity with rising
salinity (Table II).   Most salinity peaks, however, occurred between sunset
and midnight when activity was generally greatest.   Figure 7 illustrates examples
of recorded salinity fluctuations superimposed on shrimp activity curves.   Artificial

TABLE II

*A general summary of observed events from July, 1963, to May, 1964, showing pink shrimp
activity trends (general slope of activity curve) associated with salinity changes*

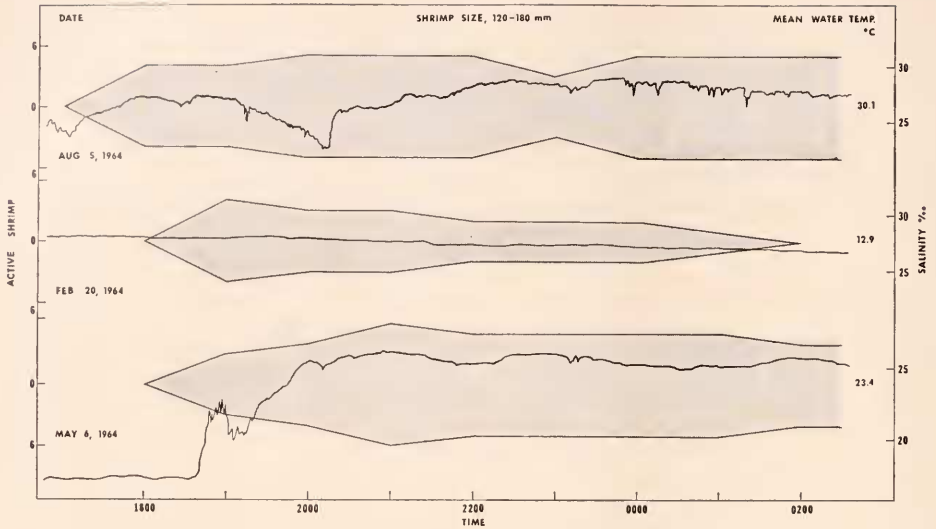| Events	General activity trends	
	Increasing	Decreasing
Increasing salinity	13	8
Decreasing salinity	12	10

FIGURE 7. Shrimp activity and salinity fluctuations. Left ordinate and shaded area = activity; right ordinate and trace recordings = *in situ* salinity.

manipulation of salinity under otherwise controlled conditions was not attempted.

Fatigue. In an attempt to evaluate the behavior of pink shrimp under conditions conducive to continuous activity, experimental animals were held in a completely dark aquarium for periods of 72 hours and observed at two-hour intervals. Section A of Figure 8 shows continuous activity (non-burrowed shrimp)
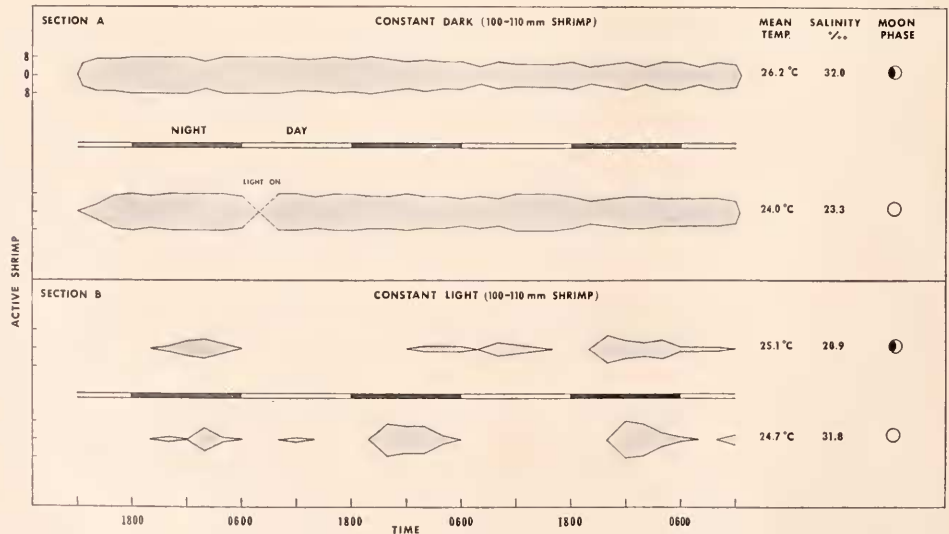

FIGURE 8. The effects of continuous dark and light conditions on the activity of pink shrimp.

with a gradual decline in magnitude under dark conditions. Temperature was maintained relatively constant (within 2° of the mean), and observations were kept to a minimum number. The ratios of total active individuals during each 24-hour period to the total active individuals within the observation series are given in Table III. The decline in activity noted under these conditions is attributed to fatigue. The effects of light are again illustrated by the dramatic changes in activity associated with covering and uncovering the aquaria and by the total interruption of activity due to an inadvertent lighting of the aquarium between 06 00 and 08 00 hours on the second day of the second series.

Availability of food. The effects of food availability on the diel activity of non-starved pink shrimp seem to be of little consequence. Twenty-four-hour aquaria observations on the activity of fed (with chopped mullet) and non-fed shrimp showed no obvious differences. Ratios of activity (activity for one group/activity for both groups) for 120–130 mm. fed to non-fed shrimp were 0.52 to 0.48, respec-

TABLE III

Activity ratios of shrimp under constant dark and light conditions

24-hour periods:	Activity ratios		
	1st	2nd	3rd
Constant dark	0.36	0.34	0.29
Constant light	0.20	0.32	0.48
Diel activity:	Day		Night
Constant dark	0.48		0.52
Constant light	0.16		0.84
Moon phase:	Full		Last Quarter
Constant dark	0.51		0.49
Constant light	0.56		0.44

tively, under conditions of constant salinity (23.0‰) and relatively constant temperature (mean temperature 20.2° C.).

To test the effect of available food on starved shrimp in relation to light, food was placed in aquaria at the end of 72-hour observations (Fig. 8). At the times food was introduced, all shrimp were burrowed and the aquaria lighted. In the dark series, ending October 2, 1964, one individual deburrowed 10 minutes after the addition of food and fed for 5 minutes before reburrowing. On October 23, 1964, two individuals deburrowed and began to feed 15 minutes after food was added. Within two minutes one of these reburrowed and a third emerged to feed. These two individuals remained active and feeding for about 30 minutes. On October 30 and November 20, 1964, after 72 hours of continuous light and little activity, only one shrimp emerged from his burrow to feed.

Diurnal cycles. Diel periodicity due to solar stimulus is obvious, and the reactions of pink shrimp to artificial light and moonlight strongly suggest external
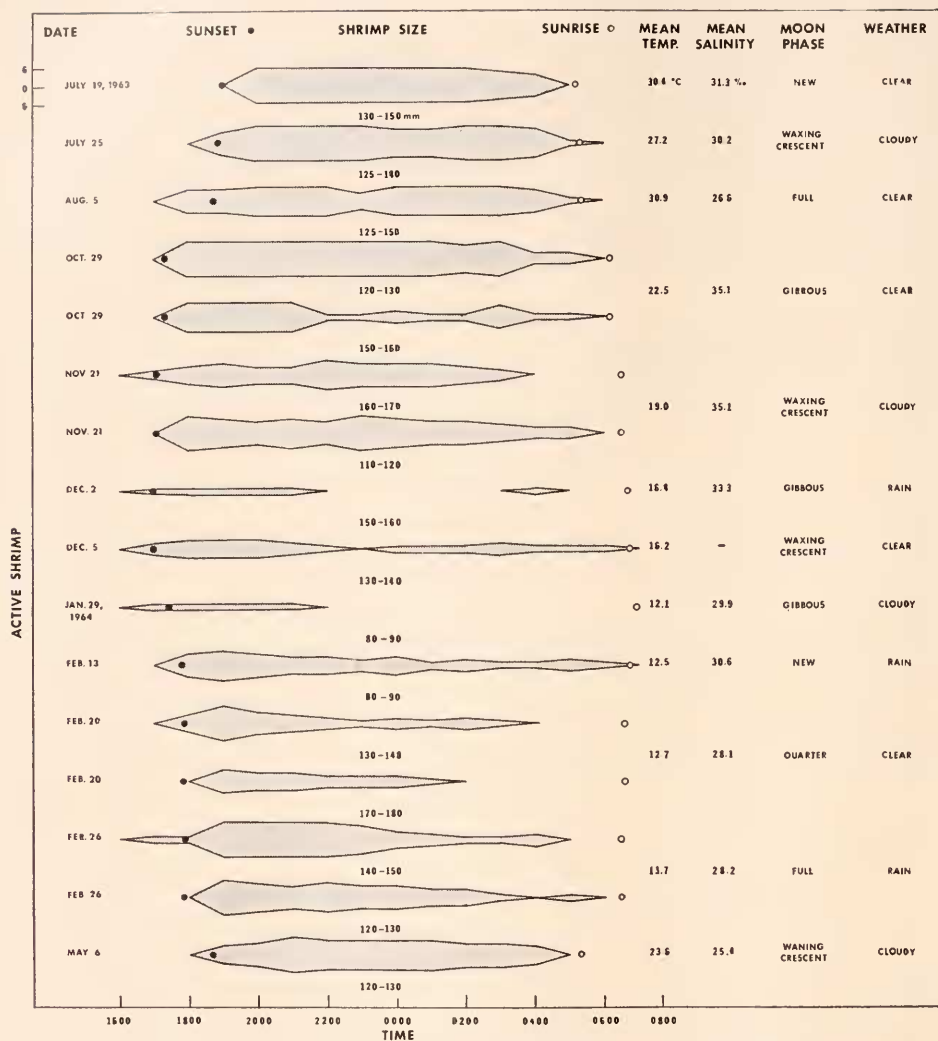
FIGURE 9. Seasonal activity cycles of selected groups of pink shrimp.

control as the primary factor. However, an endogenous component is indicated by the data presented in Section B of Figure 8. In these series, under conditions of constant light (107.64 lumens per m.²) and fairly constant temperature (within 2° of the mean), a somewhat persistent nocturnal rhythmicity is detectable. The evidence for this circadian rhythm is sketchy, but is considered worth reporting in the light of previous work on other penaeid shrimp (Dall, 1958; Racek, 1959). The ratios of all active animals for day- to night-activity are given in Table III and show the disparity between constant light and dark conditions. An increase in activity for each 24-hour period during the constant light series is also shown in Table III. The tendency for increased activity under lighted conditions with the

passage of time was noted during other shrimp studies at this station when animals were held in lighted aquaria for long periods.

Lunar Cycles. Direct correlations between lunar cycles *per se* and nocturnal activity were not well defined. Aquarium observations under constant dark and light conditions (Table III) during full and last quarter moon phases did not show strong evidence of lunar rhythmicity. Non-controlled observations from July, 1963, to May, 1964, show that 53.7% of 60 animals observed were active during the lunar phase of last quarter-new-first quarter and 44.4% of 36 animals observed were active during the first quarter-full-last quarter phase. The summary presented above was taken from observations with water temperatures above 15° C., and reflects activity between sunset and sunrise.
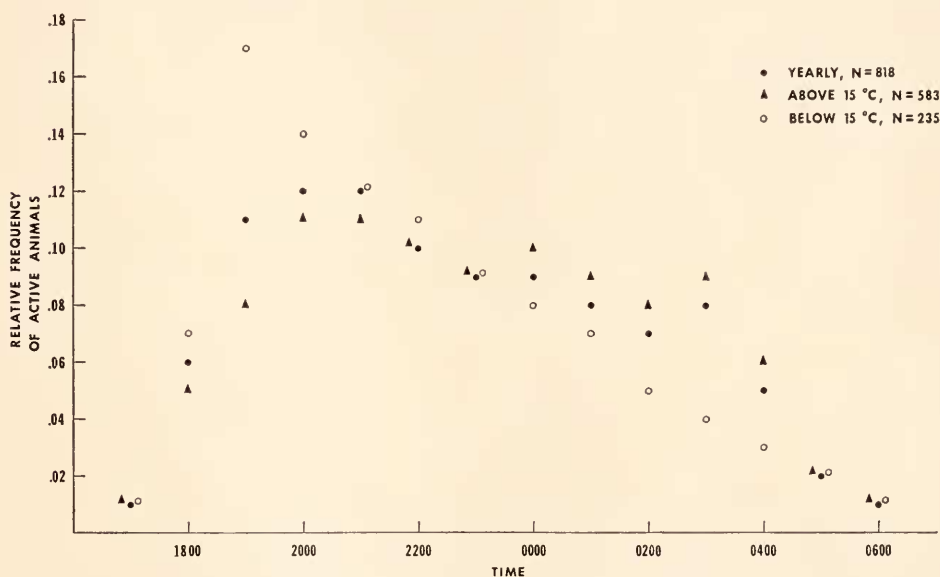

FIGURE 10. Nocturnal activity patterns reflecting photoperiod and temperature variances of the seasonal cycle.

Seasonal cycles. Figure 9 illustrates the seasonal activity cycles of selected groups of pink shrimp under uncontrolled conditions at a depth of 3 m. The duration of activity seems to be primarily controlled by photoperiods and the proportion of shrimp active at any one time by bottom water temperatures. Long winter nights are characterized by extended activity periods and a decrease in the number of active animals. Summer nights are characterized by an increase in the number of shrimp active over a shorter period. Figure 9 also indicates the ability of pink shrimp to acclimate to low water temperatures. When winter temperatures first dropped to about 16° C., (mean temperature for observation period), activity was sharply reduced. As low temperatures continued over a few months, more activity was noted even at means of 12° to 13° C.

Figure 10 shows the relative frequency of active shrimp at given time intervals to the total activity observed during all non-controlled phases of this study. The

cumulative seasonal data point to an activity peak around 20 00 to 21 00 hours, but show a considerable disparity between summer and winter nocturnal activity patterns. The difference between the two temperature groupings of animals at 19 00 (Fig. 10) could be the result of earlier sunsets during the cold season (shortened photoperiod). At temperatures below 15° C., activity data suggest a relative relationship between light and temperature. Immediately after sunset the animals become very active in the absence of light and then gradually respond to temperature and possibly fatigue by burrowing.

WATER CURRENTS AND BURROWING ORIENTATION

Observations of the effects of bottom water currents on the orientation of burrowing shrimp show that a positive rheotaxis may be expected at current velocities above about 0.2 m. per second on level bottoms. Table IV indicates that burrowing with respect to water current is fairly random below 0.2 m. per second with positively orientated individuals showing a mean burrow angle of 40° to the current axis. Above 0.2 m. per second at least 90% of the burrowing shrimp

TABLE IV

Shrimp orientation to current velocities

Current speed (m. per second)	Total no. of shrimp	% Positive orientation	% Orientation within 25° of current axis	Mean positive orientation to current axis (degrees)	*Positive orientation on either side of current axis	
					Left	Right
0.44–0.54	30	90	63	21°	12	15
0.20–0.39	35	94	45	28°	17	16
0.06–0.19	35	57	25	40°	8	12

* Individual shrimp.

orientated positive to the current, and the mean burrow angle decreased. As water currents increased there was a tendency for shrimp to burrow more nearly in line with the current axis. The data show that between 0.44 and 0.54 m. per second, 63% of the animals observed burrowed within 25° of the bottom current axis. At current velocities above 0.2 m. per second the ratio of shrimp burrowing to the right and left of the current axis was 0.52 to 0.48, respectively. Orientation to the right or left of the current axis may therefore be considered random.

During orientation studies shrimp were occasionally observed to maintain their position relative to the bottom by swimming against currents in excess of 0.26 m. per second with the pleopods providing the propulsion.

BOTTOM TYPES

Observations on the effects of bottom types in relation to burrowing were random and qualitative and made during cruises of the R/V *George M. Bowers* to various locations in the southern and eastern Gulf of Mexico. Captured shrimp were released above the bottom during daylight hours, and burrowing activity was recorded with an underwater motion picture camera.

The bottom type seemed to affect the rate of burrowing more than the degree of burrowing, with shrimp penetrating all substrates observed. Shrimp were capable of burrowing in extremely hard substrates of sand and sand-shell, and entered soft bottoms in a matter of seconds. On heavy "grass" (*Thalassia testudinum* and *Syringodium filiforme*) bottoms, adult shrimp occasionally experienced difficulty in reaching the substrate. Once on the bottom, however, the animals were able to burrow among the plant rhizomes with little effort.

Discussion

The nocturnal habits of pink shrimp have been observed and recorded in a number of earlier studies (Idyll, 1950; Viosca, 1957; Williams, 1958; Eldred, 1958; Eldred *et al.*, 1961; and Fuss, 1964), and fishermen have learned that the best catches are taken during the hours of darkness. Pink shrimp usually remain burrowed during the day, and the reason is apparently protection. Observations by swimmers during the course of this and previous work reveal that penaeid shrimp are relentlessly attacked by a variety of small and large fishes when exposed in relatively clear water. Great numbers of small pinfish (*Lagodon rhomboides*) were frequently observed attacking single large adult pink shrimp. The small fishes, often no larger than the shrimp, would immobilize their prey by biting off the appendages. Motion picture records of these attacks show the shrimp attempting to escape by burrowing.

Laboratory manipulations by other investigators concerning the effect of artificial light on activity and burrowing are somewhat contradictory. Eldred (1958) noted that during night observations hard-shelled *P. duorarum* held in aquaria immediately burrowed in the sand when exposed to green, white, and yellow lights. Aaron and Wisby (1964), in their studies of pink shrimp exposed to a 3.23 lumens per m.² white light source in an experimental apparatus, report a positive phototaxis. The results of our study show an inhibition of activity or burrowing response in the presence of light which would be expected if previous field observations (Viosca, 1957; Eldred *et al.*, 1961; Fuss, 1964) are correct. The apparent discrepancy between investigators may be due to animal size, development, and sexual maturity, or the intensity of the light used. Shrimp observed by Eldred (1958) were 82 to 102 mm., mature individuals, and in this study the animals ranged from 80 to 180 mm. Aaron and Wisby used shrimp of approximately 55 to 105 mm. ("between the leading edge of the blades and the spine of the telson"—size estimate made from Figure 2 of their paper) and state that specimen size played an important part in photic response. They showed that photoactivation (animal moved toward the light) was greatest in shrimp measuring 75 mm. and photoactic drive (animal moved through an alternating current electrical field toward the light) was least in 90-mm. specimens. Eldred *et al.* (1961) found that individuals smaller than 55 mm. were observed to be active when exposed to bright daylight or electric lights, whereas larger specimens remained burrowed.

The results of this study indicate that larger shrimp are more sensitive to light than smaller shrimp although most individuals within the size ranges observed showed a negative photic response (burrowed in the presence of daylight or artificial light). Korringa (1957) cites examples of animals that are positive to light at one level of illumination and negative at other levels. This phenomenon,

however, as a possible explanation of the discrepancy outlined above is generally unsatisfactory, as Aaron and Wisby report a positive response to 3.23 lumens per m.[2] while our results (modified *in situ*) indicate a negative response to the same value. However, Pardi and Papi (1961) state that a great many crustaceans react either positively or negatively, depending on light intensity. According to Ghidalia and Bourgois (1961) certain penaeids (*Parapenaeus longirostris, Aristeus antennatus, Aristeomorpha folicaea*) of the Western Mediterranean show a positive phototaxis in weak lunar light and negative phototaxis in intense solar light. Further detailed experiments may provide more concrete conclusions.

The most logical explanation of this variable photic behavior would seem to be size or age because photopositive reactions are generally attributed to smaller animals (below about 80 mm.) and photonegative responses to larger individuals. Pardi and Papi (1961) report that ontogenetic changes in light responses are common in crustaceans, with a greater photopositive tendency in younger stages. Ghidalia and Bourgois (1961) also noted that young shrimp usually exhibited a marked positive response, but adults showed one that was mild or even negative. The probable increased sensitivity of larger shrimp to light suggests an adaptive process which may be a prerequisite to survival in a hostile environment. Pink shrimp may well become more responsive to stimuli when they move from the protected sea grass environment of the juvenile to the open water habitat of the adult. The results of this study indicate that when males and females are about the same size there is little difference in response to light. As all of the very large specimens (170–180 mm.) were females, the apparent increased sensitivity of females is probably due to this disproportionate sex-size distribution.

SUOC observations and fishing experience leave little doubt that adult *P. duorarum* reacts negatively to solar light and generally remains burrowed during the day. The data presented here also strongly indicate that moonlight plays an important role in nocturnal activity. It is reasonable to assume that lunar light could directly influence night activity if the light threshold estimate (10^{-5} to 10^{-6} lux) cited by Waterman (1961) for crustaceans in general is valid for *P. duorarum.* The early evening burst of activity noted in SUOC observations may be associated with a period of dark-adaptation followed by increased light-sensitivity related to superposition vision and a consequent decrease in activity. Waterman (1961) reports that dark-adaption in certain crustaceans, including *Cambarus* and *Homarus,* takes about 20 minutes to an hour. The amount of moonlight penetration at depths equal to the maximum depth range (about 68 meters, Springer and Bullis, 1954) of *P. duorarum* in sufficient quantity above the estimated minimum threshold seems likely, at least under favorable weather conditions. Clarke and Wertheim [3] (1956) reported a light energy reading of about 0.001 micro watt per cm.[2] at a depth of 100 m. in the Florida current at 20 30 hours under half-moon conditions. This reading is approximately equivalent to 0.0014 lux (Roesel, 1964, personal communications) if the energy spectrum is assumed to equal that shown by Sverdrup, Johnson and Fleming (1942) for a depth of 100 m. in clear oceanic water. Even if the usual habitat of *P. duorarum* is more turbid than the Florida current, the full moon probably provides sufficient light in most cases to influence

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[3] Clarke and Wertheim also gave data on light energy measurements in turbid slope water but conversion to an approximate unit of illumination is impractical due to lack of spectra data.

activity. If the estimated minimum response of the shrimp's eye is 10^{-6} lux and the estimated maximum night light level at a depth of 100 m. is 1.4×10^{-4} lux, a response to moonlight can probably be expected. Extreme conditions of weather or turbidity would undoubtedly modify moonlight effects.

If light is the most important single factor in the regulation of pink shrimp activity, then it is necessary to explain why occasional day catches exceed night catches when turbid water is encountered. Eldred et al. (1961) and Fuss (1964) provide an explanation for this obvious inconsistency.

The influence of temperature on burrowing habits of P. duorarum has been suggested by Williams (1955) and Eldred et al. (1961), who agreed that shrimp probably remain buried in the substrate during periods of cold. Eldred has suggested that the substrate temperatures are warmer than those of the surrounding water and burrowing serves as a protective measure in the survival of the species during periods of extreme cold. Data presented here substantiate this conclusion and indicate that sudden temperature changes that occasionally occur in shallow water may cause burrowing rather than migrations to deeper water. Migrations of pink shrimp into deeper waters to avoid cold are discussed by Tabb, Dubrow and Jones (1962).

Gunter (1957) reviewed the effects of temperature on marine organisms and stated that (p. 166) "within normal limits the absolute temperature seems to have less effect than temperature changes." His statement holds true for P. duorarum. Early winter low temperature produced significant reductions in activity at levels which seemed to have little effect in late winter.

Aldrich (1964, personal communications) found a relation between the size of P. setiferus and low temperature sensitivity, with larger animals being seemingly less tolerant. Our data suggest a similar relation as evidenced by modified in situ observations on the comparative activity of large and small (relative size) shrimp under identical temperature conditions.

The complete cessation of activity at temperatures below 10° C. is supported by data presented by Eldred et al. (1961) and Williams (1955). Severe reductions in pink shrimp activity below approximately 14°–16° C. were found by Williams (1955) and by Dall (1958) for Metapenaeus mastersii. Aldrich (1964, personal communications) also found P. setiferus was adversely affected by temperatures below 12°–14° C. In general it seems that the lower temperature limit for penaeid shrimp activity is about 14° to 16° C.

Eldred et al. (1961) have also suggested that, as a protective measure, P. duorarum may burrow into the substrate during extremely high summer temperatures. Our limited observations, however, indicated that high temperatures (above about 33° C.) cause pink shrimp to deburrow, but there is a possibility that the reason was actually oxygen deficiency due to the increased water temperature. Egusa and Yamamoto (1961) have shown that P. japonicus projects its respiratory siphon above the substrate surface when environmental oxygen is reduced to 1.0 cc. per liter and came out of the bottom entirely when 0.5 cc. per liter is reached. Further work is needed on the effects of high temperatures and low oxygen tensions on shrimp burrowing behavior.

It is not surprising that salinity fluctuations within the ranges observed did not produce a marked effect on pink shrimp activity. Hoese (1960) and Gunter

(1961) disagree as to the euryhaline characteristics of *P. duorarum*, but the minimum salinities recorded in our study were considerably above the lower limits in question. Zein-Eldin and Aldrich (1964) have reported the ability of grooved postlarval penaeids (very probably *P. aztecus*) to withstand wide fluctuations of salinity, and Tabb *et al.* (1962) concluded that *P. duorarum* is tolerant to wide salinity ranges, but less so as adult size is reached. The osmoregulatory powers of *P. duorarum* have been verified by Williams (1960), who demonstrated that pink shrimp can maintain themselves fairly well for limited periods in salinity ranges of 10‰ to 30‰.

Pardi and Papi (1961), however, state that lowering the salinity of the medium generally results in photonegative reactions by marine crustaceans, and Racek (1959) concluded that prawn stocks in estuaries bury themselves when salinities decrease rapidly because of heavy rainfall. These conclusions give support to the suggested increase of activity with rising salinity noted in this study.

The results of fatiguing experiments indicate that pink shrimp are capable of extended activity under certain conditions of light and temperature, although the data do not provide information on the endurance of individual animals. Feeding trials at the end of 72-hour observation series also indicate that feeding requirements after a limited period of starvation are not sufficiently critical to overcome usual or expected diel periodicity established by photoperiods. Dall (1958) reports that *M. mastersii*, which is sensitive to light, also refused food during the day and remained burrowed. Results of continuous light observations suggest that conservation of activity will extend the ability of *P. duorarum* to undergo periods of starvation.

Other studies previously cited show *P. duorarum* is nocturnal, as did the results of earlier observations at this station (Fuss, 1964). As Brown (1961) pointed out (p. 401), "organisms dwell in a rhythmic environment," and there are many 24-hour cycles that are associated with conspicuous changes in marine habitats. The daily activity patterns of pink shrimp seem to be primarily controlled by photoperiod and other modifying environmental factors, but there is some evidence of an endogenous component. There are many excellent and exhaustive works on environmentally controlled periodicity and circadian rhythms, including those of Brown *et al.* (1955a, 1955b), dealing with fiddler crabs, in which they suggest responses to a complex of environmental stimuli and endogenous factors, and Mori's (1960) studies of the sea-pen *Cavernularia obesa*, which seems to perform rhythmic activity under the control of both environmental and physiological factors. The activity of *P. duorarum* is undoubtedly influenced by many factors and is complex in nature.

It is interesting to note that *P. duorarum* did not show a diel periodicity under controlled dark conditions, but did show some pattern of activity under constant light conditions. A similar phenomenon was recorded by Welsh (1930) in studies on the migration of distal pigment cells in the eyes of two fresh-water shrimp of the genus *Macrobrachium*. He found a persistent diurnal rhythm under constant illumination, but noted that animals kept in the dark showed no movement of the distal pigment cells. Brown (1961) has suggested a possible explanation related to the production of dark-adapting hormones as the regulatory agents that may apply here. In total darkness, fluctuations in dark-adapting hormones would not

produce changes in dark-adapted eyes. There is a possibility that the persistent rhythm component of *P. duorarum's* daily activity cycle could be related to dark- and light-adapting hormones. Dall (1958) recorded a persistent daily rhythm in the gross activity of *Metapenaeus mastersii,* as did Racek (1959) for *Penaeus plebejus.*

The increased activity with time under conditions of constant light is probably an acclimation to light rather than a quest for food, as the animals refused to de-burrow when food was introduced at the end of the series. Pardi and Papi (1961), in their review of kinetic and tactic response in crustaceans, report that light adaptation affects the sign of light responses in a number of animals, and Schöne (1961) describes conditioned learning in *Palaemonetes* and other forms.

Data derived from this study show that cessation of night activity is not as well defined as the beginning. Wheeler (1937) describes similar patterns in the swarm-ing behavior of certain prawns, including *Penaeus brasiliensis,* at the Bermuda Biological Station. As Wheeler's work was done before Burkenroad's (1939) differentiation of the *P. brasiliensis* complex, it is possible that the animal observed was actually *P. duorarum* (Gunter, 1964, personal communications). The reason for this pattern would seem to be a modifying influence of other factors, such as temperature and fatigue, on a primarily light-controlled evolution. The results of this study agree with Wheeler's (1937) conclusion that the direct action of light is the strongest inhibiting factor in diel activity of prawns, at least for this species.

Many fishermen believe that pink shrimp catches are poorer during full moon periods (Iverson and Idyll, 1959), and earlier *in situ* observations (Fuss, 1964) gave support to this theory. Our preliminary studies during the summer of 1962 were made under near-optimum water conditions for light penetration during clear weather. The present results concerning moon phase correlations are based on SUOC observations. The results are not well defined; however, they are based on much more extensive investigations, including observations in foul weather, during low bottom temperature, and in high turbidity. The studies lead to the conclusion that any moon phase correlations are directly related to light intensity and conse-quently are dependent on weather and turbidity.

Eldred *et al.* (1961) reported that moon phase showed no effect on the abun-dance of shrimp in samples, but Aaron and Wisby (1964) found that moon phase had a significant effect on the photoactivation of shrimp and that maximum photo-activation occurred during the full moon and the minimum during new moon. Our controlled observations suggest a slight activity correlation with full moon periods, but the results are not conclusive.

It would not seem unreasonable to assume that nocturnal pink shrimp are affected by moonlight if not moon phase *per se.* As Korringa (1957) has pointed out, the rhythm of the moon must be of utmost importance to marine animals that hide in their dark shelters during daylight hours, and Fox (1924) has also sug-gested that additional illumination on certain nights of the month, although weak, could cause shorter or longer periods of activity. Wheeler (1937) concluded that the coincidence of prawn swarming with the new moon is so marked that some form of correlation with the changing phase of the moon is beyond question. He suggests that the direct action of light is the clue. Racek (1959) has objected to this conclusion on the grounds that it is unlikely that the cause of periodicity in

behavior of predominantly demersal prawns is the direct inhibitory effect of light. Under conditions of extensive turbidity or inclement weather his argument is probably valid, but data presented by Clarke and Wertheim (1956) would seem to indicate that moonlight may very well control the activity of certain penaeids.

The seasonal cycles observed in this study and related to photoperiod and temperature resemble the pattern presented by Wheeler (1937) for swarming *Anchistoids*. The shift from a near bimodal summer cycle of activity to a sharp unimodal winter pattern is probably a direct result of temperature, but other factors may be involved.

Apparently no data are published on the swimming speeds or responses to water currents of penaeid shrimp. The positive orientation to water currents in excess of about 0.2 m. per second by *P. duorarum* seems to be a mechanical phenomenon, but probably also depends on optic fixation, as Hadley (1906) demonstrated with the American lobster, *Homarus americanus*. Although a detailed evaluation of the fluid dynamics associated with burrowing orientation is beyond the scope of this paper, we may assume that shrimp in contact with the bottom have a general streamlined form and show certain expected characteristics of such shapes in a fluid medium. As the water velocity increases, the shrimp should burrow more nearly parallel to the current axis and thus reduce the angle of attack and drag coefficient. When the angle of attack exceeds a certain critical value, drag increases greatly (Shapiro, 1961) and the animal experiences difficulty in maintaining position on the bottom. The angle of attack is seen to decrease with increased current velocity as reflected by the shrimp mean burrow angle.

Our observations on the burrowing ability of *P. duorarum* on various bottom types agree with previous studies (Williams, 1958; Hildebrand, 1955), and confirm the animal's ability to enter extremely coarse substrates. In one case in particular, off Panama City Beach, pink shrimp were observed to burrow in an extremely hard sand substrate in which it was difficult to force a diving knife. The animal seems to use a hydraulic mechanism in the burrowing process on hard substrates. Abdominal muscles were occasionally flexed after initial penetration, apparently forcing entrapped water with suspended sediment from beneath the burrowing shrimp.

Summary

1. The effects of certain environmental and physiological factors on the activity and burrowing habits of pink shrimp, *Penaeus duorarum*, are described.

2. Adult pink shrimp have a tendency to burrow in the presence of solar light and maximum activity does not occur until incident illumination is below 0.01076 lumens per $m.^2$ Light is apparently the most important inhibiting factor in diel periodicity.

3. Moonlight affects the nocturnal activity of pink shrimp to a limited extent but the inhibiting effects may be modified by weather and water turbidity.

4. There is a general inverse relation between nocturnal activity and water temperatures below about 26° C., and maximum activity seems to be associated with temperatures of 26° to 27° C. At water temperatures below 14° to 16° C. less than half of the animals will be active and all activity ceases below about 10° C. Shrimp apparently deburrow at temperatures above about 33° C. but remain quiescent.

5. An increase in activity with rising salinity is suggested but effects of salinity within the ranges observed (18.7–35.8‰) are probably insignificant.

6. Shrimp are capable of fairly extended activity and fatigue is probably not a limiting factor until after about 48 hours of continuous activity.

7. The need for food after limited starvation (72 hours) does not seem to overcome the activity-inhibiting effects of sunlight; and conservation of energy by burrowing will apparently extend the ability of pink shrimp to undergo periods of starvation.

8. Pink shrimp are capable of limited acclimation to light and low temperature, and large animals (above about 140 mm.) are apparently more sensitive to these factors than smaller ones.

9. Cycles of activity related to photoperiods are well defined and there is evidence of an endogenous component in the diel periodicity of pink shrimp. Persistent circadian rhythms, however, are only discernible under conditions of constant light.

10. Correlations between activity and lunar cycles *per se* are not well defined.

11. Seasonal cycles of activity seem to be primarily controlled by photoperiod and temperature. Peak daily activity during a seasonal cycle occurs at about 20 00 hours.

12. Burrowing shrimp show a positive rheotaxis in water currents at velocities above about 0.2 m. per second and as velocity increases, their burrowing angle to the current axis decreases. Orientation to the left or right of the current axis seems to be random.

13. Pink shrimp are capable of penetrating very coarse bottom types including hard sand, sand-shell, and substrates overlaid with heavy plant growth.

14. Burrowing serves as a protective measure against predators and adverse environmental conditions.

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